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Parasites, info-disruption, and the ecology of fear

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Abstract There is growing interest in the ecological consequences of fear, as evidenced by the numerous studies on the nonconsumptive, trait-mediated effects of predators. Parasitism, however, has yet to be fully integrated into research on the ecology of fear, despite it having direct negative and often lethal effects on hosts and being the most common life history strategy on the planet. This might at least be partly due to the traditional, but untested, assumption that anti-parasite responses are weak relative to anti-predator responses. To test this hypothesis, we quantified the activity and location responses of *Bufo americanus* tadpoles to one of six chemical cues: water; cercariae of *Echinostoma trivolvis*, a trematode which infects and can kill amphibians; a snail releasing *E. trivolvis* cercariae; an uninfected snail; food; or conspecific alarm chemicals signaling predation. There is also literature encouraging research on the context dependency and pollution-induced disruption of fear responses. Consequently, before quantifying responses to the chemical cues, half of the *B. americanus* were exposed to the herbicide atrazine (201 μg/l for 4 days), a reported inhibitor of fear responses in fish. Tadpoles were attracted to food, were indifferent to an uninfected snail, avoided alarm chemicals, and exhibited avoidance and elevated activity in response to a snail shedding cercariae and cercariae alone. Atrazine had no detectable effects on *B. americanus'* responses to the tested cues despite the use of a higher concentration and longer exposure duration than has been repeatedly shown to inhibit chemical cue detection in fish. The magnitude of anti-parasite and anti-predator responses were qualitatively similar, suggesting that the fear of disease and its ecological consequences could be comparable to that of predation. Consequently, we call for a greater integration of parasites into research on the ecology of fear and trait-mediated indirect effects.

Keywords Alarm chemical · Atrazine · *Bufo americanus* · Trait-mediated indirect effects · Trematode

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Introduction

There is a growing appreciation of the ecological consequences of fear (Blumstein 2006; Ripple and Beschta 2004). For instance, the mere threat of predation can induce costly changes in prey traits, such as behavior, space use, morphology, and physiology, which can then alter interactions with other species (Werner and Peacor 2003). Indeed, recent evidence indicates that these nonconsumptive, trait-mediated effects of predation can have equal or greater impacts on communities than predation itself (i.e., a density-mediated effect) (Preisser et al. 2005; Werner and Peacor 2003).

Like predators, parasites are natural enemies that can have direct lethal effects on their hosts, but they have yet to

be thoroughly integrated into the ecological literature on fear and trait-mediated effects (Raffel et al. 2008). This might be partly due to the common assumption that anti-parasite responses are weak relative to anti-predator responses, based on the observation that parasitic infections are usually less immediately fatal than a predation event (Anderson and May 1982; Dobson and Hudson 1986). This assumption, however, has not been thoroughly tested. If anti-parasite responses are similar in magnitude to anti-predator responses, this would suggest that fear induced by disease could have ecological consequences that are similar to those that have been documented for fear induced by predation (Preisser et al. 2005; Werner and Peacor 2003), opening the door to a new arena of ecological investigations.

We hypothesized that the strength of American toad tadpole, *Bufo americanus* Holbrook, responses to standardized and ecologically relevant cues signaling predation and parasitism would be statistically indistinguishable. We examined toad responses to macerated conspecifics (a general cue signaling predation) and cercariae of *Echinostoma trivolvis*, the free-living stage of this cosmopolitan trematode that infects amphibians. *E. trivolvis* can cause substantial tadpole edema and mortality related to kidney damage (Fried et al. 1997; Holland et al. 2007; Martin and Conn 1990; Schotthoefer et al. 2003), and thus there might be strong selection for toads to exhibit behaviors to reduce infection risk.

For amphibians, chemical communication is their primary sensory modality, being used to gather spatial information on both predation (Rohr et al. 2002a, 2003b) and infection risk (Kiesecker et al. 1999), as well as on the location of food (Petranka 1989), conspecifics (Rohr and Madison 2001; Rohr et al. 2002b), and heterospecifics (Sullivan et al. 2003). Further, responses to chemical cues are often fine-tuned, with individuals exhibiting responses sensitive to resource, competition, and threat levels (Petranka and Hayes 1998; Rohr and Madison 2001; Rohr et al. 2002b, 2003b).

Recent research on the ecology of fear has emphasized the importance of understanding the context dependency of fear responses (Bolker et al. 2003; Bolnick and Preisser 2005). For instance, given the importance of chemical communication for so many animals (Dodson et al. 1994), there is growing concern over pollutants inhibiting the detection of chemical information signaling danger (Lurling and Scheffer 2007). The phenomenon of pollution disrupting the transfer of vital information to organisms has been termed "info-disruption" (Lurling and Scheffer 2007). Various agrochemicals, heavy metals, and surfactants at low concentrations have been shown to be info-disruptors for numerous taxa, including amphibians (Lurling and Scheffer 2007). Hence, pollution might elevate the risk of disease and predation by altering species' perception of fear. This is an important context dependency given recent emphases on indirect effects of pollution (Relyea and Hoverman 2006; Rohr and Crumrine 2005; Rohr et al. 2006a), the context-dependent nature of trait-mediated effects (Bolker et al. 2003; Bolnick and Preisser 2005), links between amphibian trematode infections and pesticide exposure (Kiesecker 2002; Rohr et al. 2008b, c), and the role of anthropogenic environmental change on the emergence of various amphibian infections, including *E. trivolvis* (Johnson and Sutherland 2003; Rohr et al. 2008a; Skelly et al. 2006).

A well-documented info-disruptor of fish is the herbicide atrazine. Atrazine is a persistent photosynthesis inhibitor that is used globally for corn and sorghum production (Solomon et al. 1996) and is the second most commonly used pesticide in the US and perhaps the world (Kiely et al. 2004). Exposure to atrazine has inhibited chemically mediated fear (anti-predator) responses in goldfish (*Carassius auratus*) (Saglio and Trijasse 1998), impaired the ability of male Atlantic salmon (*Salmo salar*) parr to detect female priming pheromones (Moore and Lower 2001; Moore and Waring 1998), and reduced olfactory-based preference behaviors and electrical responses of olfactory neurons in juvenile rainbow trout (*Oncorhynchus mykiss*) (Tierney et al. 2007). Additionally, atrazine has caused apoptosis in a grass carp (*Ctenopharyngodon idellus*) cell line (Liu et al. 2006), indicating that it might have cytotoxic effects on fish that could influence pheromone and allelochemical production and detection.

Considering the consistent evidence that atrazine and other pollutants can act as info-disruptors in fish, we postulated that atrazine might also be an info-disruptor in amphibians, altering their perception (i.e., responses to) of the risk of predation and parasitism. To test this hypothesis and the hypothesis that the strength of standardized anti-predator and anti-parasite responses are similar in magnitude, we exposed *B. americanus* tadpoles to atrazine (or not) and then quantified their location and activity responses to chemical cues signaling food (positive control), predation (macerated conspecific), and *E. trivolvis* infection risk.

Materials and methods

Collection, maintenance, and dosing of animals

B. americanus embryos were collected shortly after hatching from a pond in Center County, Pennsylvania which was isolated from agricultural activity and atrazine inputs. *Planorbella trivolvis* snails, which harbor and shed *E. trivolvis* cercariae, were collected from a pond in Harrisburg,

Pennsylvania and were screened for echinostomatid infections as described by Kiesecker (2002). To determine the species of echinostomatid in the snails from this pond, we reared the trematodes to adulthood in golden hamsters (*Mesocricetus auratus*). We completed the life cycle of this parasite in golden hamsters and identified the adults as *E. trivolvis*. Both the tadpoles and snails were reared in aquaria filled with constantly bubbled, artificial spring water (ASW). ASW was prepared as described by Cohen et al. (1980). The tadpoles and snails were held at room temperature (20°C) on a 12:12-h light:dark cycle and fed fish flakes and frozen spinach ad libitum. At the time of the experiment all tadpoles were between Gosner stage 25 and 27 (Gosner 1960). *B. americanus* experience significant *E. trivolvis*-induced mortality during these developmental stages (Fried et al. 1997; Holland et al. 2007; Martin and Conn 1990; Schotthoefer et al. 2003; J. R. Rohr et al., unpublished data).

Four days prior to each trial, six haphazardly chosen *B. americanus* tadpoles were placed in each of 12 cups containing 500 ml dechlorinated water. Tadpoles in half the cups were exposed to 201 μg/l technical grade atrazine (99% pure; ChemService, Westchester, Pa.) dissolved in acetone (0.0002%) and the remaining tadpoles were exposed to the same amount of acetone (0.0002%) as the tadpoles exposed to the atrazine (solvent control). Six tadpoles were placed in each cup to ensure that we had at least three survivors to place in each test apparatus (gutter) for the behavioral trials. There was no effect of atrazine during the exposure period; we had nearly 100% survival during these 4 days. An atrazine exposure concentration of 201 μg/l was selected because it was the highest concentration detected in the US Geological Survey National Water Quality Database, possibly the most comprehensive freshwater pesticide monitoring study. The actual atrazine concentration of our stock solution determined by the Mississippi State Chemical Laboratory (Mississippi State, Miss.) was 196 μg/l. Previous research revealed only a minor loss of atrazine in freshwater aquaria over a 1-week period (Rohr et al. 2004), so no water changes were conducted during the 4-day atrazine exposure period. The tadpoles were fed fish flakes ad libitum during the first 3 days of atrazine and/or solvent exposure, but all food was removed on the last day of exposure so that the tadpoles would not be sated during the behavioral trials.

We only tested one high but ecologically relevant concentration of atrazine because: (1) every dose-response study we have conducted with amphibians and atrazine has produced monotonic dose-response relationships (Rohr et al. 2004, 2006b; Rohr and Palmer 2005b, Rohr unpublished data, but see Hayes et al. 2002; Storrs and Kiesecker 2004), and thus lower concentrations were expected to have less detrimental effects; and (2) each additional concentration would add six treatments to the experiment (see below) quickly making the experiment intractable. We chose to expose tadpoles to atrazine for only 96 h because this is standard in the literature for LC50 tests and because all studies demonstrating the info-disruptive effects of atrazine on fish had atrazine exposure periods less than 24 h (Moore and Lower 2001; Moore and Waring 1998; Saglio and Trijasse 1998; Tierney et al. 2007). We assumed that the longer the exposure to atrazine the more likely there would be info-disruption. Hence, we increased the exposure period to atrazine relative to these fish studies to increase the chances of detecting any info-disruption. Finally, we did not include a water control in this experiment because acetone had no effect on chemical detection of food (relative to a water control) in preliminary trials (data not shown) and similar acetone concentrations have had no detectable effects on amphibians (Rohr et al. 2003a).

Experimental design

To evaluate the effects of atrazine on responses to chemical cues signaling parasitism, predation, and food, we used a 2×6 completely randomized block design. *B. americanus* tadpoles were either exposed to atrazine or not, as described above, crossed by exposure to one of six cues: ASW (control), an uninfected *P. trivolvis* snail, a *P. trivolvis* snail releasing *E. trivolvis* cercariae, *E. trivolvis* cercariae alone, fish flakes (food resource), or two macerated conspecifics (predation cue). All 12 treatments were tested each day, there were ten experimental days (blocks), and no tadpole was tested more than once. *B. americanus* tadpoles have been shown to be attracted to chemical cues from food and to avoid chemical cues from macerated conspecifics signaling predation (Petranka and Hayes 1998; Petranka 1989), but their responses to trematode cercariae and snails have not been reported. We used the experimental apparatuses described by Rohr and colleagues (Rohr and Madison 2001; Rohr et al. 2003b) to quantify tadpole responses to these cues. The apparatus was 1-m-long gutters marked every 5 cm to create 20 equal segments. The gutters were filled with 3.5 l ASW. Each of the 12 gutters was randomly matched with one of the 12 cups holding tadpoles for the previous 4 days. Each gutter per trial received three arbitrarily selected tadpoles from its corresponding cup and these tadpoles were held in a central 5-cm-diameter cylindrical cage made of Nitex (hence, there were ten replicates per treatment, one replicate per treatment per day, and each replicate contained three tadpoles from a single cup). This cage was carefully lifted and the tadpoles were allowed to swim freely.

One hour before each trial, two *E. trivolvis*-infected snails were placed into 100 ml ASW in order to collect 1-h

worth of cercariae (the duration of the trial). These same two snails were used as the infected snails during the trials. Two uninfected snails were treated identically as the infected snails. Each cup containing 1-h worth of cercariae was poured through the open end of a 7-cm × 4-cm plastic cylinder covered in 75-μm Nitex mesh. In a preliminary trial, cercariae were placed in a 75-μm-Nitex-mesh cage set in a Petri dish with water, and none of the cercariae escaped the mesh. Hence, the mesh should have prevented the escape of the cercariae but permitted the release of chemical cues. After the cercariae were collected in the Nitex cage, the open end was covered with Nitex. Identical Nitex cages were used to hold the infected snails, uninfected snails, fish flakes (three flakes, each approximately 1 cm^2), and macerated conspecifics. To estimate the number of cercariae to which the toads were exposed during each 1-h trial, we counted the number of cercariae released by seven *E. trivolvis*-infected snails during a 1-h period on 2 separate days. These were the same seven infected snails used in the experiment. These snails released 106.7 ± 22.8 (mean ± 1 SE) cercariae/h. To prepare the macerated conspecific treatment, four American toad tadpoles were decapitated and macerated (using a mortar and pestle) just before the trial and two macerated tadpoles were placed in each of two Nitex cages.

In addition to the Nitex mesh surrounding each cage, two black window screens were siliconed at the ends of each gutter in front of the cages to prevent the tadpoles from hiding under the cages and to provide an additional assurance that there was no visual detection of the cues. Because the last segment of each gutter held cues behind a screen, the tadpoles could occupy only 18 of the 20 segments. Each cue, contained within the Nitex mesh cage, was assigned to a gutter and a gutter end in a randomly stratified manner (i.e., there were equal numbers of treatments placed on the right and left sides of the gutters and, across all trials, each treatment combination was placed on the left and right side of the gutter 5 times), and an empty, identical Nitex mesh cage was placed at the opposite end of the gutter. Having gutters with empty cages at both ends permitted us to assess the ambient activity level of the tadpoles and whether there was any directional bias in tadpole movements.

The tadpoles were provided with a 30-min pre- and post-cue acclimation period, and a total of ten trials were conducted, each of which was recorded by overhead digital camcorders. Thus, there were ten replicates for each of the 12 treatments (i.e., three tadpoles per gutter and thus 30 tadpoles exposed to each treatment combination). The gutters and cages were soaked in bleach and rinsed thoroughly after each trial to remove any residual cues, and all trials were conducted between 1030 and 1700 hours.

On comparing anti-predator and anti-parasite responses

Comparing anti-predator and anti-parasite responses is not a simple task because there are many predators and parasites that can depredate or infect a species. Also, most parasites are much smaller than predators and most hosts contain many parasite individuals of a given species, making a per capita comparison challenging and perhaps not meaningful. We chose to use macerated conspecifics because the alarm substance of toads presumably represents a general predation cue, whereas if we used any one predator species of toads our results would only be relevant to that specific predator. However, it is possible that an actual predator could elicit a stronger anti-predator response (Petranka and Hayes 1998). In an effort to standardize the comparison of anti-predator and anti-*E. trivolvis* responses, we decided to make constant the amount of time toad tadpoles were in the vicinity of a "predator" or an *E. trivolvis*-infected snail. Hence, we exposed *B. americanus* for 1 h to two macerated conspecifics, one snail shedding *E. trivolvis* cercariae, or 1-h worth of shed *E. trivolvis* cercariae. It is certainly debatable as to whether this is truly a standardized comparison of anti-predator and anti-parasite responses and there may not be an approach that will truly standardize this comparison. However, we believe that this approach is a defensible way of evaluating whether anti-parasite and anti-predator responses are at least qualitatively similar.

Video and statistical analyses

From the videos, we recorded the location of each tadpole in each gutter every 2 min to evaluate whether the tadpoles were attracted to, or avoided, the cues. We averaged the distance from the cue for the three tadpoles in each gutter and this value was used in the statistical analyses. We also recorded the number of lines within the gutter that each tadpole crossed to determine whether the cues induced any changes in tadpole activity. The average number of lines crossed for the three tadpoles in each gutter was used in the statistical analyses. We conducted ANOVA, blocking by trial, to test for the effects of atrazine, cue, and their interaction on tadpole location and activity responses. Fisher's least significant difference tests (LSD) were used to assess pair-wise responses to the cues. We predicted that tadpoles would show no attraction or avoidance response to the control (empty cage on either side of the gutter) or uninfected snail treatments but, relative to these treatments, they would avoid macerated conspecifics, cercariae, and the infected snail and would be attracted to food. Further, we predicted that atrazine would reduce these avoidance or attraction responses. We predicted reductions in activity in response to predation cues and increases in activity in response to cercarial cues, as shown previously for amphibians

(Koprivnikar et al. 2006; Rohr and Crumrine 2005; Taylor et al. 2004; Thiemann and Wassersug 2000).

Results

The location of *B. americanus* in the gutters was dependent on the cue type to which they were exposed (cue, $F_{5,98} = 7.66$, $P < 0.001$). Specifically, tadpoles were significantly closer to chemical cues from food (LSD, $P = 0.026$) and significantly avoided chemical cues from macerated conspecifics (LSD, $P = 0.004$; Fig. 1a). Tadpoles did not significantly avoid an uninfected snail (LSD, $P = 0.563$), but did significantly avoid a snail shedding cercariae (LSD, $P = 0.022$) and cercariae alone (LSD, $P = 0.003$; Fig. 1a), indicating that tadpoles were responding to parasite rather than snail cues. There was no statistically significant difference in the avoidance responses to a snail shedding cercariae, cercariae alone, or macerated conspecifics (LSD, $P > 0.428$; Fig. 1a). Previous atrazine exposure had no significant effect on any of the attraction or avoidance responses exhibited by the tadpoles (mean segments from cue ± SE, atrazine, 9.51 ± 0.43; control, 9.32 ± 0.34; atrazine, $F_{1,98} = 0.25$, $P = 0.618$, power 0.078; atrazine × cue, $F_{5,98} = 0.43$, $P = 0.829$, power 0.158).

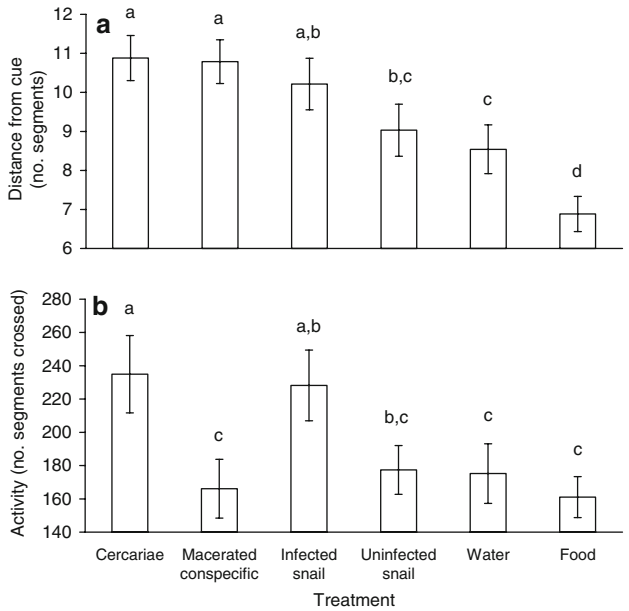

Fig. 1 **a** Location and **b** activity responses of *Bufo americanus* tadpoles to six treatments: *Echinostoma trivolvis* cercariae alone, macerated conspecifics (predation cue), an infected *Planorbella trivolvis* snail releasing *E. trivolvis* cercariae, an uninfected *P. trivolvis* snail, water (control) or food (fish flakes). Values represent mean ± SE of animals that were and were not exposed to atrazine herbicide. *Different lowercase letters* above *bars* reflect significant differences ($P < 0.05$) among treatments according to Fisher's least significant difference multiple comparison tests. The test apparatus was divided into 18 equal segments and the greater the distance from the cue the stronger the avoidance response. See text for sample sizes

Digital video discs for two of the trials were damaged and unreadable by the time we began quantifying the activity data (location data were attained from the discs first), and thus statistics for the activity data reflect fewer trials/blocks. Like the location responses, *B. americanus* activity was dependent on the cue type in the gutters (cue, $F_{5,75} = 2.99$, $P = 0.016$). Cercariae alone and an infected snail releasing cercariae both elevated tadpole activity (LSD, $P < 0.044$; Fig. 1b). The remaining four treatments were not statistically different from one another (LSD, $P > 0.603$; Fig. 1b). Overall tadpole activity was not affected by previous atrazine exposure (mean number of segments crossed ± SE, atrazine, 199.89 ± 11.25; control, 186.65 ± 11.41; $F_{1,75} = 0.91$, $P = 0.343$, power 0.156), nor did atrazine affect the specific activity response to any of the six cues (atrazine × cue, $F_{5,75} = 0.57$, $P = 0.725$, power 0.200).

Discussion

Consistent with previous research, *B. americanus* tadpoles were attracted to chemical cues from food and avoided macerated conspecifics (Petranka and Hayes 1998; Petranka 1989). In addition, *B. americanus* elevated their motor activity in response to cues released from *E. trivolvis* cercariae. *E. trivolvis* cercariae infect tadpoles by ascending through their cloaca, and increased tadpole activity can reduce *E. trivolvis* infections (Koprivnikar et al. 2006; Taylor et al. 2004), presumably by making it difficult for the cercariae to target the cloaca. It has been suggested that physical contact with cercariae stimulates tadpole hyperactivity (Taylor et al. 2004), but our study found that hyperactivity appears to be induced by the mere detection of chemical and/or vibrational cues released from cercariae. Elevated activity likely has opportunity costs and might increase predation risk (Taylor et al. 2004; Thiemann and Wassersug 2000), but this remains to be tested.

While tadpole activity and location were affected by exposure to predation- and infection-related cues, they were not influenced by exposure to atrazine, contrary to several studies demonstrating that atrazine exposure can alter the motor activity of amphibians (Carr et al. 2003; Rohr and Crumrine 2005; Rohr et al. 2003a, 2004; Rohr and Palmer 2005) and several studies showing that atrazine is an infodisruptor of fish (Moore and Lower 2001; Moore and Waring 1998; Saglio and Trijasse 1998; Tierney et al. 2007). In addition, a study on adult salamanders (*Plethodon shermani*) found no evidence that acute or chronic (28 days' exposure) atrazine exposure (0 or 300 μg/l) affected vomeronasal function or normal behavioral responses to sex pheromones or chemicals from food (Sarah Woodley, personal

communication). The info-disruption studies on fish (Moore and Lower 2001; Moore and Waring 1998; Saglio and Trijasse 1998; Tierney et al. 2007) used much lower concentrations of atrazine and shorter exposure durations than were used in the info-disruption studies on amphibians. Hence, there is presently no evidence that atrazine is functioning as an info-disruptor in the two amphibian species tested thus far and fish olfaction appears to be more sensitive to atrazine exposure than amphibian olfaction.

Care should be taken not to generalize these findings to all amphibians or pollutants or to assume that atrazine is innocuous to amphibians. For example, the insecticide, endosulfan, was shown to be an info-disruptor of newts (*Notophthalmus viridescens*), delaying male responses to female odors and inhibiting the release or potency of female sex pheromones, both of which reduced mating success (Park et al. 2001; Park and Propper 2002). Further, the mechanisms by which pollution can adversely affect organisms are numerous and complex (Relyea and Hoverman 2006; Rohr et al. 2006a). For instance, in amphibians, atrazine exposure has been shown to disrupt normal gonadal development (Hayes et al. 2002), alter growth and timing of metamorphosis (Rohr et al. 2004), elevate desiccation risk (Rohr and Palmer 2005), suppress immunity (Forson and Storfer 2006; Kiesecker 2002; Rohr et al. 2008b), increase parasitism (Forson and Storfer 2006; Kiesecker 2002; Rohr et al. 2008b), and cause direct mortality with likely delayed population-level effects (Rohr et al. 2006b).

Although there were no detectable effects of atrazine exposure, *B. americanus* did exhibit avoidance of *E. trivolvis* cercariae and an *E. trivolvis*-infected snail, behavioral alterations that should reduce infection risk and associated mortality (Holland et al. 2007; Martin and Conn 1990; Schotthoefer et al. 2003). Avoidance of areas of high infection risk is not unprecedented, but reports are uncommon. A few examples of parasite avoidance include tree frogs (*Hyla versicolor*) preferring to oviposit in pools without trematode-infected snails (Kiesecker and Skelly 2000), rainbow trout (*Oncorhynchus mykiss*) avoiding trematode cercariae that cause cataracts (Karvonen et al. 2004), and selective defecation and foraging by various vertebrates to reduce infection by fecal-oral transmitted parasites (Ezenwa 2004; Kiesecker et al. 1999).

Few studies, however, have considered the strength of anti-parasite responses relative to anti-predator responses. Here we showed that the magnitude of *B. americanus* avoidance of cercariae was qualitatively similar to their avoidance of conspecific alarm chemicals signaling predation. Although it is possible that the magnitude of avoidance would have differed if an actual predator had been used, parasites can be highly abundant and detrimental to hosts, so investment in defenses against parasites should not necessarily be lower than against predators, despite traditional assumptions to the contrary (Anderson and May 1982; Dobson and Hudson 1986). Trematode-induced avoidance and activity alterations certainly qualify as traditional "fear" responses. Hence, we call for a greater integration of parasites into research on the "ecology of fear" and trait-mediated indirect effects. Given that anti-parasite and anti-predator responses can be similar in magnitude and that anti-predator responses can have large-scale consequences for prey populations and communities (Lima 1998; Werner and Peacor 2003), it follows that anti-parasite responses should also have important consequences for host populations and communities. A few studies have provided glimpses of these potentially important trait-mediated effects. For example, *Daphnia magna* and larval damselflies (*Ischnura verticalis*) experience elevated predation risk when exhibiting anti-parasite responses (Baker and Smith 1997; Decaestecker et al. 2002), suggesting that there might be trade-offs between anti-parasite behaviors and other vital activities. In addition, two studies showed that, by altering the behavior of snails, trematodes were significant determinants of community structure and function (Mouritsen and Poulin 2005; Wood et al. 2007).

Pollution is considered the second greatest threat to aquatic and amphibious species in the United States (behind habitat loss; Wilcove and Master 2005), but is one of the most understudied stressors in conservation biology (Lawler et al. 2006), and disease might be the gravest threat to amphibians worldwide (Daszak et al. 2003; Stuart et al. 2004). We are only beginning to appreciate the intricacies of host anti-parasite responses and pollution effects on wildlife, and the importance of integrating this knowledge into management and conservation strategies (Rohr et al. 2008a, b). A more thorough understanding of the mechanisms, generalities, and consequences of info-disruption, anti-parasite responses, and heterogeneities in susceptibility to stressors might very well improve the prospects for globally declining amphibians (Stuart et al. 2004), and the many other imperiled wildlife species.

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